Landscape Ecol (2018) 33:1831–1835
https://doi.org/10.1007/s10980-018-0716-y

SHORT COMMUNICATION

An early synthesis of the habitat amount hypothesis

Charles A. Martin

Received: 22 March 2018 / Accepted: 10 September 2018 / Published online: 15 September 2018

Abstract

Context The ecological literature is filled with studies highlighting the importance of both habitat loss and fragmentation on biodiversity. The patch concept has been central to these findings, being also at the heart of many ecological theories. Recently, the habitat amount hypothesis has been proposed as an alternative, where the patch concept is put to a rest, and both patch size and patch isolation effects on species richness are reduced to a single gradient: habitat loss in the landscape.

Objectives As this theory stated clear predictions that could be experimentally tested, many formal tests of the hypothesis have been published recently and this study aims at synthesizing their results.

Methods A meta-analysis of 13 tests of the habitat amount hypothesis was conducted, to produce a single combined test of the theory.

Results The 13 tests combined suggest that effects of patch size and isolation, while controlling for habitat amounts, do exist although their overall effect is weak (r = 0.158).

Conclusions Literal interpretations of the habitat amount hypothesis, where patch size and isolation have absolutely no effect on species richness, are probably oversimplifications of the processes at work. Still, the theory could prove useful as a baseline of the effects of habitat loss, against which patch size and isolation effects must be contrasted.

Keywords Habitat amount hypothesis · Fragmentation · Meta-analysis · Biodiversity · Species richness

Introduction

Limitations in habitat availability are currently the most important threat to global biodiversity (Pimm et al. 1995), and are hypothesized to remain the largest threat in the foreseeable future (Sala et al. 2000). Accordingly, thousands of individual studies have shown the negative effects of habitat loss (Fahrig 2003). As habitat loss is not a homogeneous process, it creates all sorts of patterns in space (i.e. changes in habitat configuration), which ecology also has a long tradition of studying, from Levins' (1969) equilibrium model to the metacommunity concept (Wilson 1992; Leibold et al. 2004). Changes in habitat configuration (e.g. patch size, connectivity, etc.) are also known to have profound effects on ecosystems (Haddad et al. 2015) and we have now come to a point where habitat configuration is integrated into conservation recommendations (e.g. Strobl 1998; Rosenberg et al. 1999)

C. A. Martin (✉)
Chaire de recherche du Canada en Intégrité Écologique, Université du Québec à Trois-Rivières, 3351, boul. Des Forges, C.P. 500, Trois-Rivières, QC G9A 5H7, Canada
e-mail: charles.martin1@uqtr.ca

and is part of the reserve selection process (Margules and Pressey 2000; Briers 2002). Conservation being foremost a matter of prioritization, ecologists have long been trying to quantify the relative importance of habitat amounts and configuration for decision-making purposes, with varying results (Didham et al. 2012). The crux of the matter here being that habitat loss necessarily implies changes in configuration, and thus independent effects of either habitat amounts or configuration are often hard to disentangle.

The above conceptual model was strongly challenged when Fahrig (2013) proposed the habitat amount hypothesis (HAH), in which she questions the existence of distinct effects of patch size and isolation on species richness and implies that the effects of such patch-scale configuration metrics could be reduced to a single measure: habitat amount in the landscape. Such a bold statement came with pretty strong arguments (e.g. Fahrig found no evidence that the slopes of species area relationships were different between fragmented and homogeneous landscapes), but also important implications. The most important one being that half a century of research could have been wrongly assigning population processes to patch effects, which could have been as well explained by habitat amounts in the local landscape. The hypothesis was heavily criticized because, among other things, it was described as a phenomenological model that ignored the underlying mechanisms (Hanski 2015; Haddad et al. 2017). Fortunately, the HAH also came with clear predictions to test its claims (but see Haddad et al. 2017 about their independence). The main prediction (and probably the most controversial one) being that, while keeping the amount of habitat constant in the landscape, species richness on a plot, i.e. species density, should not increase with the size of the local patch being studied.

Since Fahrig's article was published, many research teams have tackled the task of testing the habitat amount hypothesis, and this article aims at synthesizing their results, to provide an early idea of where we stand, 5 years after the publication of the hypothesis.

Methods

I searched the Scopus database (http://www.scopus.com) on May 29, 2018, for articles explicitly testing the habitat amount hypothesis with the following query: TITLE-ABS-KEY ("habitat amount hypothesis"). From the resulting 15 articles, two were discarded as they were the seminal article and the ensuing discussion (i.e. Fahrig 2013, 2015). The remaining texts were carefully examined to ensure they were proper tests of the theory and that they (or their supplementary materials) provided numerical summaries that could be converted to a common effect size. Some studies were thus removed because they were either completed on actual islands or did not provide a metric of patch size or isolation (Piano et al. 2017; Rabelo et al. 2017; De Camargo et al. 2018; MacDonald et al. 2018). Finally, two studies were removed from the dataset because they did not provide parameter estimates or the necessary details to reconstruct them with the published information (Moreira et al. 2017; Pulsford et al. 2017). Multiple tests of the theory in the same article were considered as separate entries, provided that they were not using the same data. In case the same dataset was reanalyzed multiple ways, only the test on the most complete subset was selected. The final dataset thus contained 13 tests of the habitat amount hypothesis, from seven different articles.

For each test, I extracted either the *t*-value or *F*-value of the parameter of interest, along with either the degrees of freedom (*df*) or sample size (*n*). As *n* was needed to calculate the effect size variance (see below) and *df* were needed to convert the test statistics to a common metric, translation was made between the two (*df* to *n* or vice versa) assuming the number of parameters corresponded to the estimates provided in the results (unless explicitly stated otherwise). In three articles, *df* might have been overestimated because of the presence of random effects in the models.

In the 7 articles, the habitat amount hypothesis was tested either by assessing the existence of a slope difference between SARs of continuous and fragmented areas or by assessing the existence of independent effects of patch size or patch isolation in a model predicting species richness per sample site while controlling for the amount of habitat. Therefore, a positive relationship between patch size and species richness would produce opposite signs for the same reality, depending on the method used. The signs of the coefficients were thus adjusted so that all positive values indicate a positive effect of patch size or a negative effect of patch isolation on species richness, independent of the habitat amount.

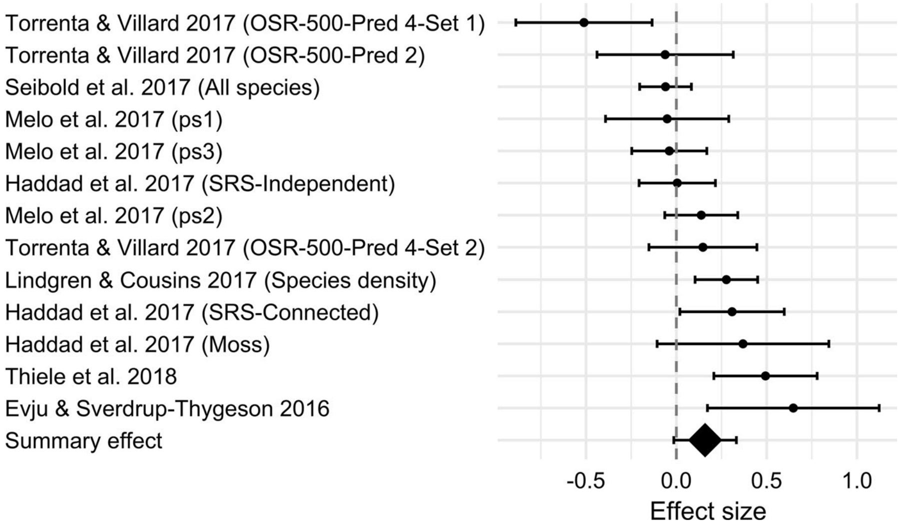

Fig. 1 Meta-analysis of the independent effect of habitat configuration on species richness, while controlling for the habitat amount in the landscape. Effect size is Fisher's z. Each row represents an individual test of the hypothesis and last row is the summary effect. Error bars are 95% confidence intervals

F-values and t-values were converted to a common metric (Pearson's r) using equations provided by Friedman (1982), using the appropriate df for each test. As Pearson's r has some problematic distributional and variance properties when computing meta-analyses, these values were further converted to Fisher's z and its corresponding variance metric (which, in contrary to Pearson's r, is independent of the z-value) using equations provided in Borenstein et al. (2009).

To compute a meta-analytic test of the habitat amount hypothesis, I calculated a weighted effect size, using the inverse of Fisher's z variance as weights in a two-level random effects model. Random intercept terms were included for each test, as well as each article, to account for the hierarchical structure of the dataset. The presence of a publication bias in the reviewed literature was assessed with Egger's regression test for funnel plots (Sterne and Egger 2005). All data analysis was completed with the metafor package (version 2.0-0, Viechtbauer 2010) in R statistical software (version 3.4.3, R Core Team 2017).

Results

Combining the 13 individual tests of the habitat amount hypothesis while accounting for the hierarchical structure of the data produced a combined effect size of 0.159 ± 0.173 (95% CI) in Fisher's z units (Fig. 1). Egger's test for funnel plot asymmetry suggests that there was no significant publication bias that could have systematically skewed this estimate ($z = 0.6526$, $p = 0.5140$; Fig. 2). This combined effect size translates to a partial correlation between species richness and patch size or isolation of 0.158 while controlling for the amount of habitat in the landscape. Cochran's measure of heterogeneity suggests that there is more variability among tests of the habitat amount hypothesis than expected by random sampling variation ($Q = 38.63$, $df = 12$, $p < 0.0001$).

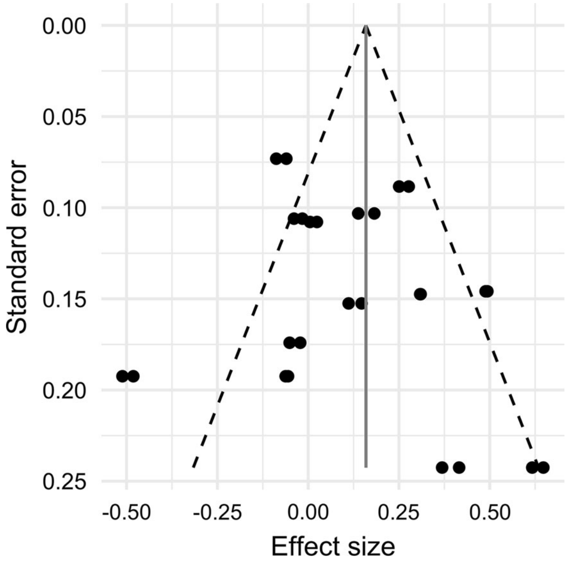

Fig. 2 Visual assessment of the publication bias in tests of the habitat amount hypothesis. Funnel represents the 95% confidence interval. Effect size is Fisher's z

Discussion

This meta-analytic test of the habitat amount hypothesis thus shows that patch size and isolation effects on species richness do exist, but they are weak (r = 0.158) once habitat amounts in the landscape are accounted for. Overall, this is more or less the same conclusion Fahrig (2003) arrived to 15 years ago in a major literature review, where habitat loss had consistent negative effects on biodiversity while habitat fragmentation per se (i.e. controlling for habitat amount) had weaker and more variable effects. This variation in the directionality of fragmentation effects was recently reassessed and, within studies where a significant effect was observed, fragmentation per se had a positive effect on biodiversity at the landscape scale in a majority of cases (Fahrig 2017), although the present synthesis shows that fragmentation-related features (patch size and isolation), measured on the local patch, have generally neutral or negative effects on its species richness. Many reasons could explain such discrepancy, one of which being that fragmentation at the landscape scale, in addition to any possible negative effect, can also increase heterogeneity (Seiferling et al. 2014), an often cited biodiversity driver (Stein et al. 2014). Mechanisms usually invoked to support the heterogeneity-biodiversity relationship include increases in habitat diversity (i.e. number of niches; Tews et al. 2004) and increases in the number of habitat types available within an organism's home range, which some species require or benefit from (i.e. complementation; Law and Dickman 1998). Such benefits of fragmentation per se cannot be captured when the studied guilds are limited to a single habitat type, as required in the habitat amount hypothesis (e.g. forest interior and forest edge species should not be studied together according to the HAH).

Despite the above-mentioned general conclusions about the direction of fragmentation effects, the high amounts of between-study heterogeneity in the test results also support another common idea in landscape ecology, which is that configuration effects are both context (Andrén 1994; Thompson et al. 2002) and taxa specific (Bender et al. 1998; Prugh et al. 2008). Consequently, the development of further tests of the HAH in additional contexts should be strongly encouraged, as it is likely that each context could provide its own unique answer to the question.

Keeping in mind that this synthesis is based only on a handful of tests, it hints that a literal interpretation of the habitat amount hypothesis, where changes in patch size and isolation have absolutely no effect on species richness when accounting for habitat amount in the landscape, is probably an oversimplification of the actual processes at work and misses important context-specific issues. Just like when Hubbell's (2001) unified neutral theory of biodiversity reversed the burden of proof on ecologists to show environmental effects on community structure against a background of neutral processes, Fahrig's habitat amount hypothesis should probably be viewed as a baseline of habitat loss effects, above which habitat configuration effects must be contrasted to be considered as important.

The dataset generated and analyzed during the current study along with related computer code are available in the FigShare repository, https://figshare.com/s/45649772e9cd166b293d.

Acknowledgements Thanks to Raphaël Proulx, Vincent Maire and Lael Parrott for stimulating discussions on the subject. This manuscript was greatly improved by insightful reviews from Lenore Fahrig, Nick Haddad and Jessica Lindgren. The author acknowledges a grant from Natural Sciences and Engineering Research Council of Canada (NSERC).

References

Andrén H (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71:355–366

Bender DJ, Contreras TA, Fahrig L (1998) Habitat loss and population decline: a meta-analysis of the patch size effect. Ecology 79:517–533

Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2009) Introduction to meta-analysis. Wiley, Chichester

Briers RA (2002) Incorporating connectivity into reserve selection procedures. Biol Conserv 103:77–83

De Camargo RX, Boucher-Lalonde V, Currie DJ (2018) At the landscape level, birds respond strongly to habitat amount but weakly to fragmentation. Divers Distrib 24:1–11

Didham RK, Kapos V, Ewers RM (2012) Rethinking the conceptual foundations of habitat fragmentation research. Oikos 121:161–170

Evju M, Sverdrup-Thygeson A (2016) Spatial configuration matters: a test of the habitat amount hypothesis for plants in calcareous grasslands. Landscape Ecol 31:1891–1902

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40:1649–1663

Fahrig L (2015) Just a hypothesis: a reply to Hanski. J Biogeogr 42:993–994

Fahrig L (2017) Ecological responses to habitat fragmentation Per Se. Annu Rev Ecol Evol Syst 48:1–23

Friedman H (1982) Simplified determination of statistical power, magnitude of effect and research sample sizes. Educ Psychol Meas 42:521–526

Haddad NM, Brudvig LA, Clobert J, Gonzalez KF, Holt RD, Cook WM (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. Sci Adv 1:e1500052–e1500052

Haddad NM, Gonzalez A, Brudvig LA, Burt MA, Levey DJ, Damschen EI (2017) Experimental evidence does not support the Habitat Amount Hypothesis. Ecography (Cop) 40:48–55

Hanski I (2015) Habitat fragmentation and species richness. J Biogeogr 42:989–993

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Law BS, Dickman CR (1998) The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. Biodivers Conserv 7:323–333

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Loreau M (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecol Lett 7:601–613

Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bull Entomol Soc Am 15:237–240

Lindgren JP, Cousins SAO (2017) Island biogeography theory outweighs habitat amount hypothesis in predicting plant species richness in small grassland remnants. Landscape Ecol 32:1895–1906

MacDonald ZG, Anderson ID, Acorn JH, Nielsen SE (2018) Decoupling habitat fragmentation from habitat loss: butterfly species mobility obscures fragmentation effects in a naturally fragmented landscape of lake islands. Oecologia 186:11–27

Margules C, Pressey R (2000) Systematic Conservation Planning. Nature 405:243–253

Melo GL, Sponchiado J, Cáceres NC, Fahrig L (2017) Testing the habitat amount hypothesis for South American small mammals. Biol Conserv 209:304–314

Moreira EF, da Santos RL, Silveira MS, Boscolo D, Neves ELD, Viana BF (2017) Influence of landscape structure on Euglossini composition in open vegetation environments. Biota Neotrop 17:1–7

Piano E, Isaia M, Falasco E, La Morgia V, Soldato G, Bona F (2017) Local versus landscape spatial influence on biodiversity: a case study across five European industrialized areas. Environ Monit Assess 189:126

Pimm SL, Russell GJ, Gittleman JL, Brooks TM (1995) The Future of Biodiversity. Science 269:347–350

Prugh LR, Hodges KE, Sinclair ARE, Brashares JS (2008) Effect of habitat area and isolation on fragmented animal populations. Proc Natl Acad Sci USA 105:20770–20775

Pulsford SA, Lindenmayer DB, Driscoll DA (2017) Reptiles and frogs conform to multiple conceptual landscape models in an agricultural landscape. Divers Distrib 23:1408–1422

R Core Team (2017) R: A language and environment for statistical computing. R Core Team, Vienna

Rabelo RM, Bicca-Marques JC, Aragón S, Nelson BW (2017) Are fluvial islands "real" islands for arboreal mammals? Uncovering the effect of patch size under the species–area relationship. J Biogeogr 44:1802–1812

Rosenberg KV, Rohrbaugh RW, Barker SE, Hames RS, Lowe JD, Dhondt AA (1999) Land manager's guide to improving habitat for scarlet tanagers and other forest-interior birds

Sala OE, Chapin FS III, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Leemans R (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774

Seibold S, Bässler C, Brandl R, Fahrig L, Förster B, Heurich M, Müller J (2017) An experimental test of the habitat-amount hypothesis for saproxylic beetles in a forested region. Ecology 98:1613–1622

Seiferling I, Proulx R, Wirth C (2014) Disentangling the environmental-heterogeneity–species-diversity relationship along a gradient of human footprint. Ecology 95:2084–2095

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecol Lett 17:866–880

Sterne JA, Egger M (2005) Regression methods to detect publication and other bias in meta-analysis. In: Rothstein HR, Sutton AJ, Borenstein M (eds) Publication bias in meta-analysis. Prevention, assessment and adjustments. Wiley, Chichester, pp 99–110

Strobl S (1998) Towards a list of science priorities for the conservation and management of southern Ontario forests—Results of a workshop. For Chron 74:838–849

Tews J, Brose U, Grimm V, Tielbörger K, Wichmann M, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J Biogeogr 31:79–92

Thiele J, Kellner S, Buchholz S, Schirmel J (2018) Connectivity or area: what drives plant species richness in habitat corridors? Landscape Ecol 33:1–9

Thompson FR III, Donovan TM, DeGraaf RM, Faaborg J, Robinson SK (2002) A multi-scale perspective of the effects of forest fragmentation on birds in eastern forests. Stud Avian Biol 25:8–19

Torrenta R, Villard MA (2017) A test of the habitat amount hypothesis as an explanation for the species richness of forest bird assemblages. J Biogeogr 44:1791–1801

Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. J Stat Softw 36:1–48

Wilson DS (1992) Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73:1984–2000